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XXV. *Electro-Physiological Researches.—Fourth Memoir. The Physiological Action of the Electric Current. By Signor* Carlo Matteucci, *Professor in the University of Pisa, &c. &c. Communicated by* Michael Faraday, *Esq., F.R.S., &c. &c.*

Received June 11,—Read June 18, 1846.

In my Treatise upon the Electro-Physiological Phenomena of Animals, at page 230 I have described the following experiment:—" I prepare a frog after the method adopted by Galvani, separating the junction of the two thigh-bones, and placing them so divided between two glasses, with the claws immersed in these glasses. Introducing the conductors of a pile of from sixty to eighty pairs in both the glasses, I pass a current through the frog, which is direct in one limb and inverse in the other. After a lapse of from fifteen to twenty minutes, I establish a communication between the glasses by means of a wire, whereupon the limb traversed by the inverse current immediately contracts. On quickly removing the communicating wire, no contraction whatever occurs." I concluded from this experiment that the action of the electric current, in weakening or destroying the excitability of the nerve, was not the same whatever were its direction, and that the direct current acted with a much greater energy than the inverse. This fact appeared to me to be of sufficient importance to warrant further investigation, and I think that the results at which I have arrived will serve to throw some light upon that difficult subject, the physiological action of the electric current. I felt convinced, in the first place, that it now behoved me to employ means for the investigation of these phenomena far more exact than those I had hitherto resorted to. Every natural philosopher who has ever so little studied the contractions caused by the passage of the electric current upon the nerves of a frog, prepared for the purpose, must certainly have perceived how very difficult it is to arrive at satisfactory results, where the force of the contraction excited is to be judged of by the eye. In this manner our knowledge is limited to the fact, that when the excitability of the nerve is lessened, the direct current causes contractions only at the very moment in which it begins to circulate, whilst the inverse current produces contraction only at the moment of its ceasing to pass. In one word, we can only judge of these phenomena by their presence or by their cessation. But in what relation these effects vary, in what order, as regards intensity, the phenomena of the first period of excitability of the nerve are transformed into those of the second period; what relation the number of the contractions produced bears to the strength of the current, to its duration, &c., are so many questions which we shall never be able to solve without an apparatus by which to measure the contractions caused by

the passage of the current. The apparatus which I have employed is that which Mons. ARAGO presented to the Académie Royale des Sciences, in the sitting of the 17th of September 1844, and the construction of which is due to the talent of Mons. BREGUET. The apparatus principally consists of a solid brass support AB (fig. 1.)

Fig. 1.

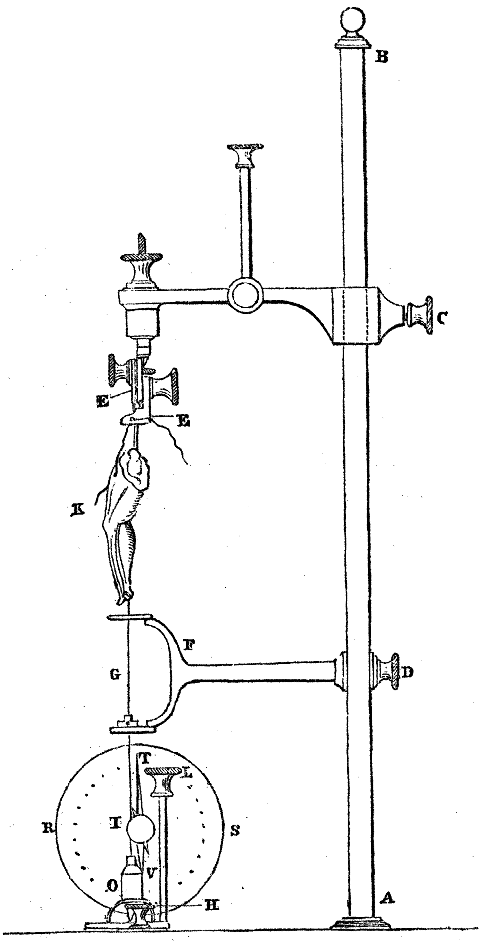


Fig. 2.

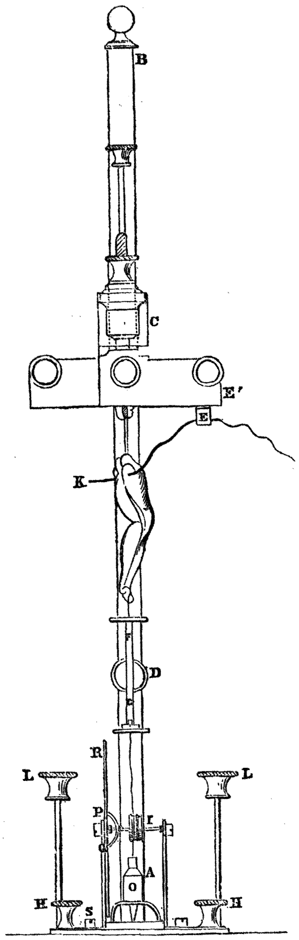
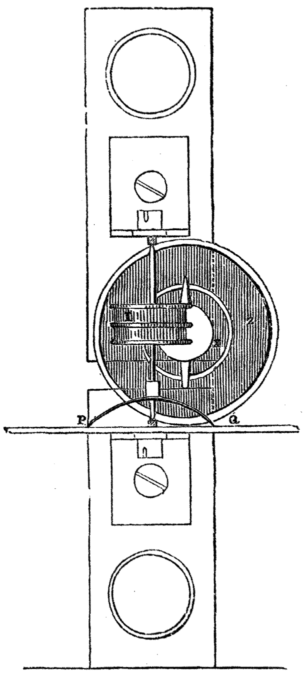
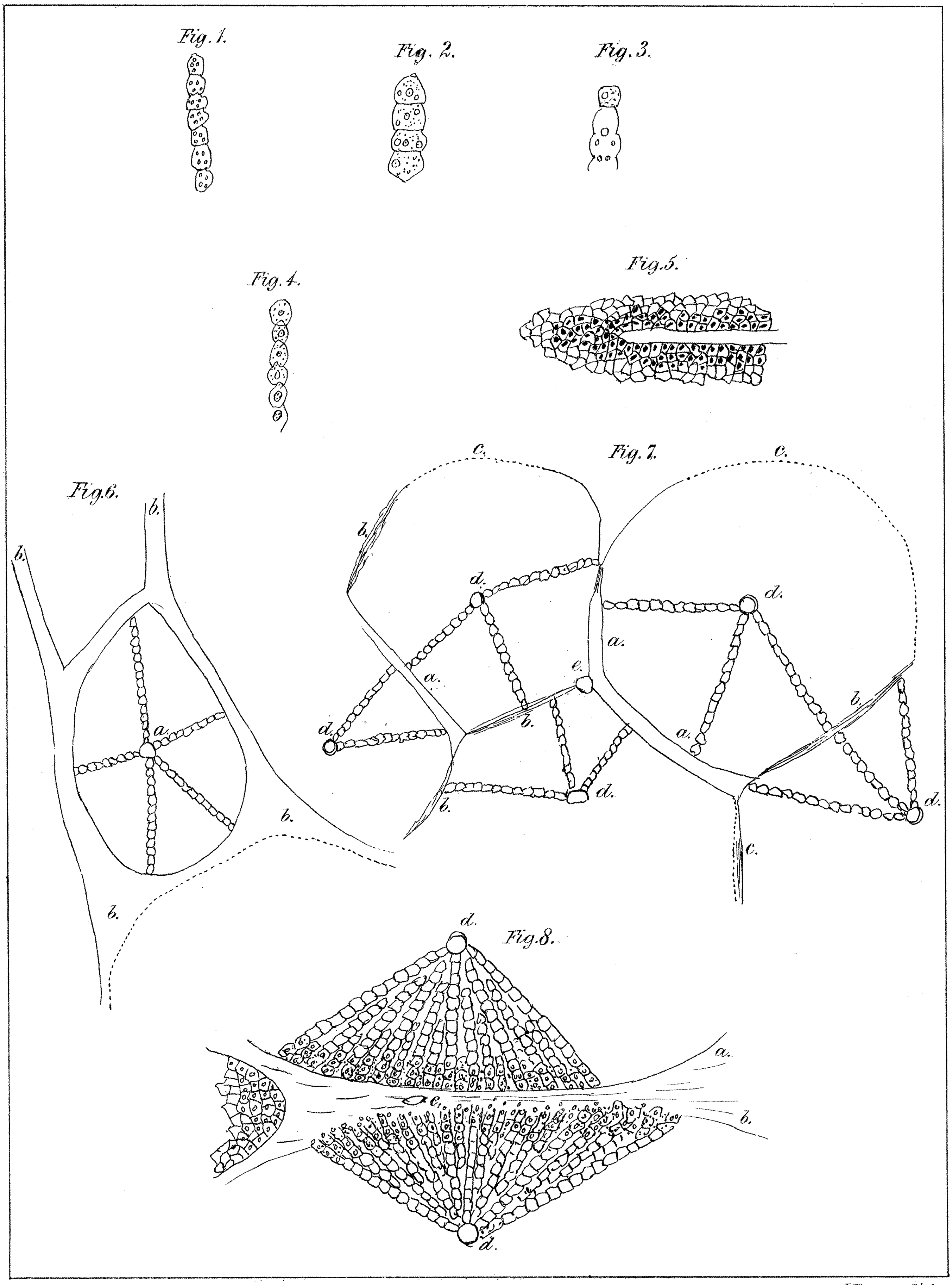


Fig. 3.



fixed upon a wooden stand, in which slide two pieces of metal C, D capable of being fixed in different places by means of screws of pressure (*vis de pression*). The piece of metal C is furnished with a vice E, in which is to be held the morsel of spinal marrow of the prepared frog, and is fastened there by three screws. The other piece F, of a forked shape, is provided with a hole in each extremity of the fork, in which a very fine wire G is fixed or regulated. At one end of the wire is a hook to which is affixed the claw of the frog, the other end of the wire is attached to a silken thread which winds round the little pulley I. Upon this pulley another thread of silk is wound, in contrary sense to the former, and to this is attached a small leaden weight O. The axis of the pulley is furnished with a kind of double index PQ, in the form of a semicircle. The axis is fixed upon two pivots, which admit of being



J. Basire, lith.

more or less approximated. One of these pivots is the centre of a circle RS, which bears a division. A long ivory needle TV is attached to this pivot; it is very light, and turns with thé slightest possible touch. The use of this ivory index is obvious. In effect, when this index is brought in contact with the semicircular one PQ, which is attached to the axis of the pulley, and the pulley is put in motion, the movement is communicated tho te ivory index, and this latter will stop at the point at which it arrives in its gyration even when the pulley is brought back to its former position by the little weight. It must be allowed that without such an index as the one described, it would have been impossible to have judged of the extent of the movement of the pulley produced by the contraction, on account of its short duration. The weight I have been in the habit of using is 0·600 gramme, sufficient to allow of the limb returning to its position after the contractions have ceased; a heavier weight than this would stretch the nerve too much. The following is a description of the manner in which I pass the current. In every case it is always a half frog, deprived of the muscles and bones of the pelvis, which is used for this experiment. The half frog is thus reduced to a portion of spinal marrow, which is held in the vice, the nervous filament, the thigh and the leg, minus the claw, which is cut off. The little hook of the wire G is inserted between the bone and the tendo-achillis. Lastly, a gilded steel needle is thrust into the muscles of the thigh, as near as possible to the insertion of the nerve; and to this needle is soldered a very fine copper K covered over with silk, which is fixed to the piece of ivory E. It is quite clear that in order to pass the current through the nerve, nothing more is wanting than to touch the support AB with one pole of the pile, in any point whatever, and the wire which is soldered to the steel needle with the other pole. In all my experiments I made use of a WHEATSTONE pile, the elements of which, as everybody knows, are formed of an amalgam of zinc, contained in a cylinder of wood immersed in a solution of sulphate of copper in which the copper of the pile dips. I suppress here a great number of small details which are essential to complete success in the experiments, but which naturally present themselves to any person repeating them with some degree of care. One thing is very certain, which is, that it will ever be impossible to make any advance in the study of the physiological action of the electric current, without having recourse to processes which give the measure of that action.

The phenomenon which first engaged my attention is that which I had already observed, and which is referred to at the commencement of the present memoir. I have frequently repeated the experiment, varying the force of the current and the duration of its passage, and have found the results invariably the same. At the outset of the experiment, the two limbs, direct and inverse, are seen to contract both at the commencement and on the cessation of the current. After some minutes, varying from fifteen to twenty, according to the vigour of the animal, and especially according to the force of the current, the difference in the contraction of the two limbs manifests itself, that is to say, the leg traversed by the inverse current con-

tracts only on breaking the circle, whilst the leg traversed by the direct current contracts only on closing it. The duration of the passage of the current, which is necessary for the production of these phenomena, is less in proportion as the current is stronger. If the passage of the current be continued through the same frog, it ends in the production of but one contraction, which is that which takes place on breaking the circuit, in the limb traversed by the inverse current. It is essential to the production of this latter phenomenon, to prolong the passage of the current more or less, from twenty to forty minutes, according to the strength of the current. I have frequently seen the contractions of the inverse limb prolonged, under the influence of a feeble current, and subsisting after four hours that the circuit had been kept closed.

I was anxious to ascertain whether these phenomena could be produced equally well by limiting the passage of the current to the lumbar nerves alone. In this view I wrapped very thin laminæ of tin round two nerves of the frog prepared in the manner above described, taking care to roll the laminæ round the nerves as close as possible to their points of entrance into the thighs. On passing the current, precisely the same phenomena as those already described are observable. The only difference that can be distinguished is in the duration of the passage of the current which is necessary for producing contraction only in the inverse limb, on breaking the circuit. This duration is less in this case than in the preceding experiments. This difference is easily accounted for, by taking into consideration the diminished resistance of the circuit in such a disposition, and comparing it with that of the circuit formed by the entire frog. Of this fact I have been enabled to satisfy myself completely, by introducing a galvanometer in the two circuits. The difference between the two currents, the same pile being used, is so great that it is impossible to entertain any doubt upon the subject. Since, then, the current is strongest when the nerve only is traversed, the phenomena corresponding to the different periods of excitability of the nerve ought to be obtained in a shorter time. I hardly need say that the manner of obtaining these phenomena, described at the commencement of this memoir, is identical with that which I have mentioned. In effect, the current in the frog may just as easily be checked or renewed by taking out and replacing the poles of the pile in the liquid in which the frog's paws dip, as by joining the two liquids by means of a metallic arc, and by removing the communication. Nevertheless it may not be useless to mention an experiment having reference to this, which it is as well to be acquainted with. I assume that the frog is prepared in the manner described, and subjected for a sufficient time to the passage of the current, so that contraction takes place only in the inverse limb, and on breaking the circuit. This being the case, while the circuit is closed, let a drop of pure water, or salt water, serum, blood, or any other conducting liquid, be dropped upon each of the two nerves separately. The drop produces no effect upon the nerve traversed by the direct current, while the contraction of the limb whose nerve is traversed by the inverse current

is the immediate consequence of the contact of the liquid with this nerve. No such effect follows the contact of oil or turpentine with the nerve. It is very evident that the conducting liquid bathing the nerve stops the current in the nerve itself, being a better conductor. The contact of a muscular mass with the nerve produces the same effect as a liquid conductor. All this proves that the conducting power of the nerve is inferior to that of muscle and of distilled water.

I have repeated the above experiments upon living frogs. I prepared them in such a manner as to leave the two limbs united to the back by the lumbar nerves alone. I suspend this frog by hooks fixed to his lower jaw, and I pass the current from one paw to the other. I repeated the experiment frequently, and have always observed that after a certain time, varying from twenty-five to forty minutes, the inverse limb alone contracted on breaking the circuit. Thus it appears that it requires a somewhat longer time to produce the same effect with the electric current upon the nerve of the living animal, than upon the dead one.

It thus remains clearly proved that *the passage of the electric current through a mixed nerve modifies the excitability of this nerve in a very different manner, according to its direction: the nerve traversed by the direct current loses its excitability much more rapidly than that which is traversed by the inverse current.* I ought here to add, that hitherto we have no experiment proving that a nerve subjected to the passage of the inverse current loses its excitability otherwise than it would have done if merely left to itself. I return to the exposition of facts. Out of ten frogs submitted to the experiment above described, frequently eight at least present the following phenomenon:—On breaking the circuit after the current has circulated twenty-five or thirty minutes, the inverse limb alone contracts; but this contraction does not cease immediately after the circuit is broken. The inverse limb continues to be contracted, exhibits, that is to say, symptoms of *tetanus*. I have frequently witnessed the contractions lasting from ten to twenty seconds. If without waiting till the contractions cease the circuit is again closed, the limb, which was stiff and contracted, will be observed to give one more violent contraction when the circuit is in the act of being closed, and then immediately return to its natural state. It is not a rare occurrence to find frogs which present these phenomena after a lapse of three or four hours of experiment. These phenomena exhibit themselves equally when the passage of the current is confined to the nerve alone, to the exclusion of the muscle*. There is one observation which it is important to make with reference to the phenomena just alluded to. I have repeatedly stated that when the current has circulated for twenty-five or thirty minutes in the prepared frog, the only contraction is that of the inverse limb on opening the circuit. The circuit may be frequently

* This strong and enduring contraction which seizes the inverse limb upon breaking the circuit, offered me a favourable opportunity of witnessing the phenomenon of induced contraction. The nerve of the galvanoscopic frog should be stretched upon the muscles of the thigh of the inverse limb. On breaking the circuit the galvanoscopic frog becomes contracted, and *persists in this state as long as the inverse limb remains contracted.*

broken and closed again, and there will be but that one contraction visible: there never will be any contraction either in the direct or in the inverse limb on closing the circuit. If the current be then passed for a certain time longer, on opening the circuit we shall have the persisting contraction already alluded to. On re-establishing the circuit during this tetanic condition, the inverse limb is convulsed for an instant, and then regains its natural state. This is the circumstance to which I wished to call attention: the contraction in the inverse limb on closing the circuit (which had previously ceased), *reappeared* when the phenomenon of the persisting contraction manifested itself.

It is now time to speak of what happens if the nerves, after having been acted upon by an inverse current, circulating through them for some time, be then subjected to the influence of a direct current, or one taking an opposite direction. This case, which belongs naturally to the voltaic alternatives, is easy to foresee. The contraction subsists, but only at the moment of closing the circuit. As regards the limb which has been traversed by the direct current, on subjecting it to the inverse current, two things may occur equally easy to foresee. If the passage of the direct current through the nerve has been of long continuance, so that there is no contraction when the circle is closed, nothing takes place on passing the inverse current; there is no contraction on breaking the circuit. If, on the other hand, the passage of the direct current has not been too protracted, so as not to entirely destroy the excitability of the nerve, on passing the inverse current the contractions reappear on breaking the circuit. It will be seen in the course of this memoir, that it is clearly proved by experiments the most exact, that the contractions exhibited in this case increase within certain limits proportionally with the time of the passage of the inverse current. I shall reconsider these phenomena in the course of this paper, and at present limit myself to the conclusion that *the inverse current is not endowed with the property of destroying the excitability of the nerve; that in some cases it is clearly shown by experiment that this excitability is reproduced by the passage of that current, and that, on the contrary, the direct current easily destroys the excitability of the nerve.*

Lastly, I directed my experiments in the view of ascertaining the difference of excitability of the nerve due to the electric current according to its direction, by substituting the ordinary stimulating agents for provoking it, in the place of electricity. The following experiments admit of being easily verified. The frog is prepared in the usual manner, and is disposed for the experiment in the way so frequently described. The passage of the current is continued until there is no contraction except in the inverse limb on breaking the circuit. Arrived at this point, the passage of the current is to be interrupted, and each nerve is to be touched separately with caustic potassa, or better still with a heated iron; the result is so constantly the same that the direction of the current passed through the two nerves may even be told by it. The effect of the caustic potassa, or heated iron, upon the inverse nerves is merely that of pro-

ducing contraction. The conclusions which we have drawn are very general: *the excitability of a nerve is modified by the electric current according to its direction*; and when we reflect that the passage of the inverse electric current through the nerve of an animal deprived of life, prolonged for two or three hours, produces on ceasing a very violent and persisting contraction, and that when this happens it has re-acquired the property, which it had lost before, of provoking contraction at the moment the inverse current begins to be passed, and that finally the passage of the direct current, for a time relatively very short, entirely destroys the excitability of the nerve, we are led to believe that *the action of the current upon the excitability of the nerve is opposite for opposite directions*. This is the point I wished to establish by experiments of measure, and I hope that I have satisfactorily demonstrated the fact. I began by measuring the contraction with BREGUET's apparatus, which I have described. It was important to determine and compare the contractions excited by the direct and by the inverse currents*, principally taking into account the duration of the passage of the current. In all these experiments the same nerve must never be submitted to the action of both the direct and the inverse currents. My mode of operating is this. I prepare the frog in the ordinary manner, and after having divided the pelvis from the rest of the trunk, I separate it into two parts, so that the two limbs remain united by the lumbar nerves attached to a portion of spinal marrow. I fix this piece of the spinal cord in the vice, and in this manner I am enabled to pass the current in either nerve *ad libitum*. By repeating a great number of experiments, sometimes beginning with the direct, at other times with the inverse current, it is not difficult to obtain a table of numbers which agree with one another as well as could be expected in this kind of experiment. I always leave the circuit open as short a time as possible between one experiment and another. A certain degree of practice enables the experimenter to employ only as short a time as two seconds in bringing the ivory index back into position. In the same way the shortest possible time for leaving the circuit closed is two seconds, for this is exactly the same time required for replacing the needle which had been removed from its position by the first contraction. The numbers which follow are the degrees of the division of the dial of the apparatus. It is unnecessary for me to give all the numbers resulting from my experiments; it will be sufficient to cite some of them in order to show the course of the phenomena. The following experiment proves the weakening of the excitability of the nerve owing to the passage of the direct current. Each passage of the current was prolonged for sixty seconds, and the following numbers give the measure of the contraction obtained each time the circuit was closed. These numbers are 16, 12, 10, 8, 4, 2, 2, 1. The inverse current was next tried on the other limb. On prolonging the passage of the current for two seconds I obtained a contraction of 10°. I left the circuit closed for sixty minutes, and still the contraction was 7 on opening the circuit. Thus far these numbers merely show the principal fact upon which I have insisted so strongly,

* Both at the commencement of the current and on its ceasing.

which is, *the very different rate of reduction of the excitability observable in two nerves, one of which is exposed to the passage of the direct, the other to that of the inverse current.*

It was very important to compare the excitability of a nerve subjected to the passage either of the direct or of the inverse current, with that of a nerve left to itself for an equal time. The results at which I invariably arrived are these: we are sure when employing the direct current that there will no longer be any contraction after the passage of the current has been kept up for fifteen or twenty minutes. With the inverse current, on the contrary, we have just seen that after a much longer passage of the current, the contraction produced on breaking the circuit was not greatly inferior to that which takes place in a nerve quite fresh, and having experienced the action of the current for only two seconds. The following are the numbers given by one nerve left untouched, and another exposed to the inverse current. I submitted to experiment a nerve left to itself; and twenty-five minutes after the preparation of the limb I passed the inverse current for the shortest possible time, and on opening the circuit the contraction was 20°. The other nerve, exposed to the current for twenty-five minutes without intermission, gave 18° on opening the circuit. In another experiment the numbers were 16° and 12° for a passage of thirty-five minutes. Repeating the same experiment with the direct current, I never remarked any perceptible contraction on breaking the circuit and reclosing it immediately. It is just to observe that the natural decrease of strength, independent of the passage of the current, ought to be greater for the nerve subjected to the experiment, and which is always somewhat stretched by the weight of the limb, than for the nerve which is left in a state of repose.

It is easy to prove that the passage of the inverse current in a nerve acts for a definite, though a very short time in producing an increase of excitability, which for the same reason disappears very quickly after breaking the circuit. To prove this I shall commence with an exposition of the experiments instituted for measuring the contraction produced, as well on closing as on breaking the circuit of the inverse current. We know, in general, what happens in this case. In the first place, when the nerve is very excitable, there is contraction both on closing and breaking the circuit, and little by little the former contraction disappears completely. The following numbers were obtained on leaving the circuit closed for two seconds, and open for that time. At first a contraction of 20° both on closing and on breaking the circuit; at the expiration of ten minutes there was no contraction on closing the circuit, but one of 12° on breaking the circuit. At the end of thirty minutes things were precisely the same. The following are the numbers obtained from another experiment under the same circumstances, but upon a nerve which had already lost much of its excitability.

Contraction on closing the circuit.	Contraction on breaking the circuit.
20°	20°
12	18
4	16
2	16
0	12
0	12
id.	12
	12
	12
	id.

When the nerve is very excitable the action of the inverse current may be proved to be proportional to the time of its passage, making the passage in one case excessively short. In effect, when the nerve is endowed with a very high degree of excitability, the contraction produced on breaking the inverse circuit, whether it be for one second, for twenty seconds, or even for thirty seconds, is always the same; but the case is no longer the same when the current is passed for a shorter time than one second. Unfortunately I have not been able to employ an apparatus for measuring the duration of the passage of a current for a shorter time than one second. The way I arrive at these results is this: instead of establishing the circuit by dipping one of the conducting wires of the pile in the same recipient of mercury in which is the other wire, I hold them both in my hands and bring them rapidly in contact with one another. The numbers obtained from various experiments and with different frogs are 22°, 24°, 28° of contraction, on breaking the inverse circuit, and these numbers were the same whether the current were passed for one second only, or as long as twenty seconds or thirty seconds. On touching one wire with the other very quickly, the contractions in the same circumstances were only 4°, 6°, 8°.

When instead of a nerve, the excitability of which is very great, we choose for our experiments one in which this is considerably diminished, it is easy to prove that the contraction produced by the inverse current ceasing to pass increases, within certain limits, proportionally to the time of the passage of the current. To bring the nerve to this state of excitability, it may be either left to itself for a long time, or be stimulated by frequent intermitted currents in rapid succession. Before detailing the results which follow, it is necessary to mention what happens when a nerve has been exposed for a long time to the passage of the direct current, or to repeated actions of this current in those cases in which the nerve is left to itself. In fact, in order to be able to measure what is due to the action of the inverse current, we must first know what is the effect upon the nerve of its being left to itself, after the direct current has ceased to act upon it.

Marianini had already found that a frog which has lost the faculty of contracting upon passing the current, re-acquires it on being left to itself for five seconds. I have

studied these phenomena anew, measuring the contractions in a frog subjected for some minutes to the passage of the direct current: the contraction, which was 20° at the commencement of the experiment, was but 8° at its conclusion on closing the circuit, and 0° on breaking it. The interval of time that the circuit remained open was a little less than two seconds, that is to say, the shortest time for the experiment; in the same manner the circuit was left broken the shortest time possible. I next varied the time of the circuit remaining incomplete. The following are the results obtained: for two seconds of repose, 10°; for three seconds, 11°; for five seconds, 12°; for ten seconds, 12°. Where the nerve has lost still more of its excitability, the effect of the repose is protracted still longer. Upon a frog, the nerves of which had been traversed by the direct current during thirty minutes, 2° of contraction followed upon breaking the circuit and again closing it immediately. After two seconds of repose, the contraction was 6°; after three seconds, 6°; after fifteen seconds, 7°; after thirty seconds, 8°. The time, therefore—always very short—that the nerve is left unacted upon by the current, and in which it acquires all the excitability which it is capable of regaining, is so much the shorter as its excitability is greater. I must add, that the increase of excitability produced by the repose of a nerve which has been stimulated by the direct current, persists in this same nerve for a time admitting of being measured, even after it has been again subjected to the passage of the direct current. There were 2° of contraction on closing the direct circuit, which had already been closed for thirty minutes. Leaving the circuit open for fifteen seconds, then closing it, the contraction was 8°; then closing the circuit immediately, and leaving it closed as short a time as possible, I opened and again closed as quickly as possible, and the contraction was 6°. Proceeding in the same manner, and passing the direct current for four seconds, the contraction was 3°, for five seconds only 2°, as at the commencement. A very short time of repose is sufficient to restore to the nerve as much as it can regain of that excitability which it had lost by the passage of the direct current; in like manner a very short time of the passage of this current will dissipate the increase of excitability acquired by repose. In general, the duration of these actions is in the inverse ratio of the degree of excitability of the nerve.

We now pass on to those experiments which prove incontestably that *the excitability of the nerve is increased by the passage of the inverse current, and that, within certain limits, proportionally to the duration of the passage of this current.* After having arranged a frog in my apparatus, I pass a direct current through the lumbar nerve for thirty minutes; I then wait until all contraction from the passage of the direct current has ceased, and that even after having left the nerve in repose for thirty seconds or sixty seconds. I then pass the inverse current, which scarcely ever occasions any contraction on closing the circuit, but on leaving the circuit closed for a longer or shorter time, there are different degrees of contraction on breaking the circuit. The following are some of the numbers obtained. In one case, after passing

the inverse current for two seconds, 4°; after five seconds, 6°; after thirty seconds, 10°; after 120 seconds, 10°. With another frog, which had been very long under the influence of the direct current, the contractions, after passing the inverse current for two seconds, 0°; after passing the current ten seconds, 0°; sixty seconds, 1°; 120 seconds, 2°. In another experiment, at the expiration of two seconds of the passage of the inverse current, contraction 0°; after a passage of five seconds, 3°; twenty seconds, 8°; fifteen seconds, 10°; thirty seconds, 10°. In a fourth experiment, the duration of the inverse current and the degrees of contraction were as follows:—two seconds, 0°; three seconds, 3°; ten seconds, 6°; fifteen seconds, 8°; thirty seconds, 10°; sixty seconds, 10°. In all these experiments I left as short an interval of time as possible between each such successive current.

It has been already seen what takes place when the inverse current is passed, and the nerve is endowed with a very high degree of excitability: the passage of the inverse current for only one second suffices, in such a case, to restore to the nerve all the excitability it is capable of acquiring. To distinguish the phenomenon we are now considering upon a nerve in the state of excitability alluded to above, the inverse current should be made to act for very small fractions of seconds.

Next in the order of our investigations, we are led to examine whether this augmented excitability of the nerve, produced by the passage of the inverse current, can persist, even after the cessation of this current, or whether, on the contrary, it can have no existence beyond the period that the nerve is under the immediate influence of the current. It has already been mentioned, that when the direct current has been made to act for twenty-five or thirty minutes, so as no longer to produce any contraction, on passing the inverse current there is scarcely ever any contraction on closing the circuit. This contraction, which is always the first to disappear, may still be reproduced, but to effect this it would be necessary that the passage of the inverse current should be prolonged considerably, and that the circuit should remain open as short a time as possible. In effect, every time that the frog presents the phenomenon of persistent and tetanic contraction, that is to say, after the inverse current has been passed for a considerable time, a contraction takes place on closing the circuit, and the tetanic convulsion ceases on the instant. It is therefore proved that this increase of excitability, produced by the passage of the inverse current, persists for a very short time when the nerve is very excitable, while this persistence increases with the diminution of the excitability, and with the duration of the inverse current. The same law is therefore always verified according to the different degree of excitability of the nerve.

A few experiments, conducted in a different manner, lead to the same conclusion. I pass an inverse current for some time through the nerve of a frog disposed in my apparatus; I then break the circuit, and leave it so for a time varying for each experiment. I close the circle, and always again break it immediately, and note down the contraction which follows. The circumstance which varies in all these experi-

ments, is the longer or shorter repose given to the nerve which has previously been acted upon for a considerable time by the inverse current. In one of these experiments the contraction was 14° on opening the inverse circuit which had been long closed. Leaving the circuit incomplete for five seconds, and then completing it and breaking it again immediately afterwards, the contraction was only 4°. Again, I complete the circuit, and on breaking it, after the inverse current has been passed for ten seconds, the contraction again amounts to 14°. In another experiment it was also 14° on opening the inverse circuit, which had remained closed during 120 seconds. Opening the circuit, and after two seconds closing, then breaking it immediately afterwards, the contraction did not exceed 10°. Then closing again, and allowing the current to pass for sixty seconds, the contraction again became 14°, as in the beginning. Breaking the circuit again, and leaving the nerve in quiet for sixty seconds, I complete the circuit and open it again immediately, and the contraction does not exceed 8°. In another experiment, on opening the circuit after the nerve had been acted upon by the inverse current for sixty seconds, the contraction amounted to 18°. I then left the nerve in repose for five seconds, after which, closing the circuit and breaking it again immediately, the contraction was 12°. After twenty-five seconds of repose the contraction was 8°: finally, leaving the inverse circuit closed for five seconds, the contraction, on breaking the circuit, was again 18°, as at the commencement. It is therefore also proved by these as well as by all the former experiments, that *the increased excitability produced by the passage of the inverse current persists after the current has ceased for a time varying in length, according to the primitive excitability of the nerve*; if the excitability of the nerve is very great, the increase produced by the passage of the inverse current ceases immediately, or almost immediately, after breaking the circuit; while it persists longer if the excitability of the nerve is already weakened.

Up to this point we have only studied the action of the inverse current upon the mixed nerves of the prepared frog, so that the increase of excitability produced by the passage of the inverse current must necessarily be in some measure hindered by the weakening of this excitability, the consequence of death. It was therefore necessary to study the action of the inverse current upon a living animal. At page 200, and in the following pages of my Treatise on the Electro-Physiological Phenomena of Animals, I have described some experiments of this kind, which I have subsequently repeated. When a current from a pile, direct or inverse, is passed along the sciatic nerve of a live rabbit, it always occasions violent contractions of the lower limbs and of the entire trunk; the animal screeches and agitates itself. These phenomena present themselves equally with the direct and with the inverse current, both at the commencement and at the end; but a difference very soon appears if the circuit remains closed. With the direct current the contraction is soon over, and the leg alone contracts when the circuit is closed. With the inverse current the symptoms of pain remain when the circuit is closed, as also the contraction in the leg when the

circuit is opened. The experiment may be prolonged for several hours with the same results.

The following experiments were performed for the purpose of comparing together the contractions caused by the direct and inverse currents at the instant of closing the circuit in both cases. The frog in these experiments was prepared in the manner described, then cut in half, and a nerve of one half was acted upon by the direct current, and a nerve of the other half by the inverse current. The experiments were repeated several times, first passing the direct current, at one time, through one half of the frog, and afterwards the inverse through the other half, or reversing this order. The following are the numbers obtained:—

Number of experiments.	Contraction on the introduction of the direct current.	Contraction on the introduction of the inverse current.
1	16°	8°
2	16	4
3	14	6
4	18	12
5	16	12
6	24	8
7	20	16
8	8	4

Although the correspondence between the numbers in the two columns is far from being constant, it is nevertheless proved in a very evident manner, that the contraction caused by the introduction of a direct current upon a mixed nerve, which has not been previously stimulated by the current, is always stronger than that which follows the introduction of the inverse current. The result is the same if a discharge of the Leyden jar is used to provoke the contraction; that is to say, a very slight shock from the Leyden jar, if direct, will cause contraction, and which would be insufficient to effect this if inverse.

While repeating the experiments referred to in the above table, I took occasion to note down the contractions which took place on opening the circuit of the inverse current. The contraction so produced is never stronger than that which occurs the first time that the direct current is passed. Both contractions are in general similar if the nerve is very excitable, and the inverse circuit left closed for a very short time. When the excitability of the nerve is considerably diminished, the inverse current must be made to circulate for a much longer time, to produce, on opening the circuit, the same contraction as that caused by the introduction of the direct current.

I will now sum up, with a few general conclusions, the results of all the experiments hitherto cited.

1. The passage of the electric current through a mixed nerve produces a variation in the excitability of the nerve, differing essentially in degree, according to the direction of the current through the nerve. This excitability is weakened and destroyed,

and that more or less rapidly, according to the intensity of the current, when it circulates through the nerve from the centre to the periphery (direct current). The excitability, on the contrary, is preserved and increased by the passage of the same current in a contrary direction, that is to say, from the periphery towards the centre (inverse current).

2. These variations in the excitability of the nerve, produced by the passage of the current, tend to disappear more or less rapidly on the current ceasing. If the nerve is taken from a living animal, or from one in which life is but just extinct, so that its excitability is very great, these variations only last as long as the current continues to pass; while they survive the cessation of the current by from one second to ten seconds or fifteen seconds, if the nerve has already lost some of its excitability.

3. If the same current be made to act upon a mixed nerve, the contraction which occurs on the first moment of its introduction is very different, according to its direction: the direct current always occasions a stronger contraction than that which is due to the inverse current.

In another memoir, which will be a continuation of the present, I propose to investigate, as far as is possible, the cause of this diversity of action of the current according to its direction in a nerve. The conclusions drawn above will, I hope, suffice for the present to form a much simpler theory of the physiological action of the electric current than that we have at present, if it be true that we have any at all.

All are aware that a spark is emitted on the instant the circuit of a pile is closed, and again on breaking the circuit. It is also well known that the spark emitted on breaking the circuit increases if the circuit is composed of an electro-magnetic spiral with its cylinder of iron. Let it be remembered that there is no sign of the current passing when the circuit continues closed; to produce contraction the circuit must be broken or closed anew. The simplest idea then which we can admit, and which is demonstrated by experiment, is that muscular contraction is excited in every case by the electric spark. That which might perhaps have appeared to be in opposition to the admission of this idea, is the fact of the frog contracting from very feeble currents. It is very easy to overthrow this difficulty. In fact, I may dispense with any further repetition of experiments by recalling VOLTA's opinion in support. Immediately after GALVANI's first discovery, VOLTA applied himself to the study of the action of the discharge of the jar upon the nerves of frogs and other animals; and in his very first memoir upon Animal Electricity, he declares that the prepared frog is without comparison the *most sensitive electrometer we possess.* In one of his experiments he found that a charge at all times sufficient to excite contractions could not be estimated at the $\frac{1}{20}$th of a degree of his straw electrometer. Indeed it is very easy to verify these assertions of VOLTA. My plan is as follows:—I take a small Leyden jar having about thirty square centimetres of coating, and after having charged it to saturation, I discharge it four times successively with a metallic rod, so as at last to produce no perceptible spark. In the same manner, at this

point there is no sign given by the electrometer with a dry pile. I then place the prepared frog astride between the balls of the universal discharger, and establishing a communication between the coating of the jar and these two balls, very strong contractions of the frog follow. Continuing this operation in precisely the same manner, and producing successive discharges of the same bottle through the frog, I never obtain less than twelve contractions, and in some cases I have even had as many as twenty. The first fact which strikes our attention in these experiments is that which Volta himself did not fail to observe. The most feeble discharge, said Volta, directed from the nerve to the muscle, and which provokes contraction, is but the one-fourth or even the one-sixth of that which is necessary to produce contraction when directed from the muscle to the nerve. This difference we are enabled to measure more exactly by acting with the electric current. In order to repeat this experiment of Volta with greater facility, and at the same time in a more conclusive manner, I confined myself to making the discharge act upon the nerve alone in the following manner. The frog is prepared in the ordinary manner, the pelvis divided, and it is stretched upon an isolating plane; the two extremities of the universal discharger are so disposed as only to admit of the discharge circulating through the nerves and the portions of spinal marrow. Thus one nerve is traversed by the direct discharge and the other nerve by the inverse. I have always used the same bottle after having discharged it with the metallic arc. After the first contractions, which are excited equally in both limbs, that limb only continues to contract which is traversed by the direct discharge. These results occur equally when nerves, which have not previously been subjected to any discharge, are acted upon. This is easily put to the proof by merely discharging the bottle several times through other frogs before beginning to act upon those which had been purposely put aside without the shock being passed through them. It is soon seen, after a few touches, that that limb alone contracts the nerve of which was exposed to the action of the direct discharge.

We may therefore conclude that the action of electricity upon the mixed nerves of an animal living or recently killed, is reduced to the two following facts:—

1. The electric discharge traversing a nerve awakens muscular contraction; but this contraction is much stronger when produced by the direct discharge than when it is excited by the inverse discharge.

2. The electric current circulating through a nerve of a living animal, or an animal newly killed, produces a variation in the excitability of the nerve: if the current is direct, the excitability is diminished and destroyed; while, on the contrary, the excitability is preserved and increased by the passage of the inverse current.

It is needless to observe that these latter phænomena can be verified in the dead animal only within such limits as are necessarily fixed by the cessation of the vital conditions essential to the preservation of the properties of the nerve. It will be ob-

served that I have not taken any account in this memoir of the sensations awakened by the passage of electricity in the nerve.

To complete this memoir, it only remains for me to show how the different phenomena, produced by the passage of the electric current through the nerve, may be arranged in groups founded upon the two principles quoted and deduced immediately from experiment. In this manner I hope to redeem my pledge of giving a theory of the physiological action of the electric current. It is only in this manner that the advance of the physical sciences can be promoted, by deducing, that is to say, the greatest number of facts possible from the smallest number of elementary facts. I do not indeed pretend to affirm that the two principles upon which I take my stand, and which are immediately deduced from experiment, are the simplest and most elementary facts in so vast a field as that of the connection between the electric and nervous phenomena; but it is certain that a great number of electro-physiological facts, which existed without any mutual relation, are now brought under the dependence of two fundamental facts. The manner in which a mixed nerve, subjected to the passage of the electric current, presents different phenomena according to the degree of its excitability, is this. In the first period of its excitability it is natural that the contraction should take place, whatever be the direction of the current in the nerve. On breaking and on closing the circuit, the electric discharge, which if the pile were strong enough would be accompanied by a spark, always takes place whatever be the direction of the current; consequently there ought to be contraction in every case. When the excitability of the nerve comes to be diminished, either by the passage of the current, according to the law which has been established, or naturally, the effects of the electric discharge can no longer be the same; when the direct current has been passed for some time there will be no contraction produced by the discharge which accompanies the breaking the circuit. By degrees, as the excitability becomes naturally enfeebled in the nerve, the contraction proceeding from the discharge, which takes place on closing the inverse circuit, will be found to disappear. From the excitability produced in the nerve by the passage of the inverse current, contraction will be produced by the discharge which accompanies the breaking of the inverse circuit. The alternatives of Volta may be explained in a like simple manner. A nerve, of which the excitability has been destroyed by the passage of the direct current, reacquires its lost excitability under the action of the inverse current; and it is thus that contraction should occur on breaking the inverse circuit, when there was no contraction on closing the direct circuit. According to the state of the nerve, the increase of excitability persists or subsides immediately after the passage of the inverse current. If the latter case occurs, there is never any contraction except on breaking the inverse circuit, while in the former case the contraction may likewise occur on closing the inverse circuit. It is invariably the case that the strongest of these two contractions is that which accompa-

nies the breaking of the inverse circuit. It is scarcely necessary to say, that if the nerve has been previously traversed by the inverse current, before subjecting it to the passage of the direct current, the contraction in this case ought to be much stronger than that which took place before on opening the circuit. The unequal effect, according to the direction of the same discharge through a nerve, has been clearly demonstrated by experiment. VOLTA and MARIANINI have studied the voltaic alternatives by passing the current through muscular masses and along nerves, but without acting separately upon one nerve with the direct and another with the inverse current. Thus it happens, that in this way of operating, in the same muscular mass there are some nervous filaments traversed by the direct current, and others traversed by the inverse current. Starting from this principle, it is easy to refer the fine experiments of VOLTA and MARIANINI to the explanation which we have already given of the voltaic alternatives.

Pisa, March 22, 1846.